THE UPPER PALAEOZOIC TETRACORAL GENERA *LOPHOPHYLLIDIUM* AND *TIMORPHYLLUM*

by JERZY FEDOROWSKI

ABSTRACT. The morphology of *Lophophyllidium*-like genera and their relationships are described and discussed. In early growth stages, *Lophophyllidium* has a zaphrentoid arrangement of septa with an elongate counter septum; the genus is characterized by a pseudocolumella that is extremely variable in morphology, both ontogenetically and between individuals; septal microstructure is trabecular. The synonymy of *Lophophyllidium* includes *Sinophyllum* Grabau, *Malonophyllum* Okulitch and Albritton, *Stereostylus* Jeffords, *Agarikophyllum* Fomitshev, and *Khmerophyllum* Fontaine; each was originally distinguished on the basis of pseudocolumella morphology.

Timorophyllum differs from *Lophophyllidium* in ontogeny and microstructure; macrostructural similarities reflect homeomorphy.

SPECIMENS having a pseudocolumella are the most common components of the Permian tetracoral fauna from the Glass Mountains, Texas. The extraordinary individual variability of some species of *Lophophyllidium* and a study of the type material of the genera *Lophophyllidium*, *Stereostylus*, *Lophamplexus*, *Malonophyllum*, and topotypes of *Timorphyllum* led to the conclusion that the first four genera are synonyms.

A complete study of phylogeny and the species of the discussed genera is beyond the scope of this paper. The main purpose is to show the variability of some skeletal elements of this group of corals and to indicate that some of these elements are not generic characters in the group discussed.

Only papers about *Lophophyllidium*-like or *Timorphyllum* corals that include new or controversial opinions are discussed. Some opinions of other authors, which coincide with mine are not discussed. Species descriptions will be included in a monographic study of Glass Mountains tetracorals, now in preparation.

Figured material is housed in the United States National Museum (USNM) and the Kansas University Museum (KUM).

THE SYSTEMATICS OF *LOPHOPHYLLIDIUM*

Genus LOPHOPHYLLIDIUM Grabau, 1928

Type species. Cyathaxonia prolifera McChesney, 1860.

Synonyms. Cyathaxonia McChesney, 1860 e.p., *non* Michelin *in* Gervais, 1840.

Lophophyllum White, 1875, 1877, 1884; Martin, 1881; Keyes, 1894; Stuckenberg, 1904 e.p.; Duerden, 1906; Lorenz, 1906; Brown, 1909; Grabau, 1922; Morningstar, 1922; Soshkina, 1928 e.p.; Kelly, 1930; Huang, 1932; Yoh and Huang, 1932; Merla, 1934; ?Vojnovsky-Krieger, 1934, *non* Milne-Edwards and Haime, 1850.

Sinophyllum Grabau, 1928.

Malonophyllum Okulitch and Albritton, 1937.

Soshkineophyllum Moore and Jeffords, 1941, *non* Grabau, 1928.

Stereostylus Jeffords, 1947.

Agarikophyllum Fomitshev, 1953.

[Palaeontology, Vol. 17, Part 3, 1974, pp. 441–473, pls. 60–70.]

Khmerophyllum Fontaine, 1961.

Rotiphyllum Ivanovsky, 1967, *non* Hudson, 1942.

Stratigraphic and geographic range. Lower Carboniferous to Upper Permian, cosmopolitan.

Diagnosis. Solitary corals without dissepimentarium; ontogeny zaphrentoidal, with cardinal septum unshortened in youngest stages; axial end of counter septum is the main component of pseudocolumella but either axial tabellae or septal lamellae or both may be additional elements; minor septa extremely variable in length; growth lines in septa very steeply arranged; trabeculae very short, ordinarily crossing two growth lines only.

Review of the synonymized genera

Lophophyllum Milne-Edwards and Haime, 1850 (type species: *L. konincki* Milne-Edwards and Haime, 1850). The taxonomic position of this genus and its morphology was preliminarily discussed by Lecompte (1955) who considered it to be a distinct genus which differs from *Koninckophyllum* in lacking dissepiments. I agree with Lecompte's conclusions and disagree with Carruthers's (1913) concept of this genus which was based on erroneously identified material. Consequently, all species having a dissepimentarium were excluded from this study. Many of the species assigned to *Lophophyllum* were discussed by Schouppé and Stacul (1955). Most of the other species that lack a dissepimentarium and have a pseudocolumella belong to *Lophophyllidium* (see synonymy in Schouppé and Stacul).

Lophophyllidium Grabau, 1928 (type species: *Cyathaxonia prolifera* McChesney, 1860). Grabau (1928, p. 99) following Carruthers (1913) wrote: 'The corals of *Lophophyllum proliferum* type cannot be considered congeneric with *Lophophyllum tortuosum*.' The correctness of this position is not in doubt, although Huang (1932, pp. 22, 23) disagreed with it. Huang, however, presented mostly historical and nomenclatural arguments. The ontogenetic development of *C. prolifera* was described by Duerden (1906). A neotype for this species was chosen by Jeffords (1942) but this neotype and most of the original syntypes are probably lost. The last two syntypes have been restudied and one has been illustrated (Pl. 60, fig. 1; Pl. 62, fig. 1*a–c*; Pl. 63, figs. 4, 5). Moore and Jeffords (1945) established the family Lophophyllidiidae. Both genus and family (sometimes as a subfamily) are generally accepted. The most complete synonymy of the genus was given by Scrutton (1971), who agreed that the structure of the pseudocolumella was not taxonomically significant.

Sinophyllum Grabau, 1928 (type species: *Lophophyllum pendulum* Grabau, 1922). Grabau (1928, p. 100) proposed the new generic name for corals having septa accelerated strongly in counter quadrants and a 'pseudocolumella formed by the excessive thickening of the original pali-columella, which still remains as the central lamina. In section the pali-columella shows a zone of radial structure or an irregular series of rod shaped bodies.' He also indicated that the axial end of the counter septum wraps around the pseudocolumella in some stages of growth (Grabau 1928, pl. IV, figs. 1*c*, 3*c*). The last feature is very common in many of the later described species of *Lophophyllidium*-like corals. Huang (1932) and Wang (1947) studied topotypes of the American *Cyathaxonia prolifera* and compared the structure of its pseudocolumella with that of *Lophophyllum pendulum* Grabau, 1922. Both authors did not see any differences between these

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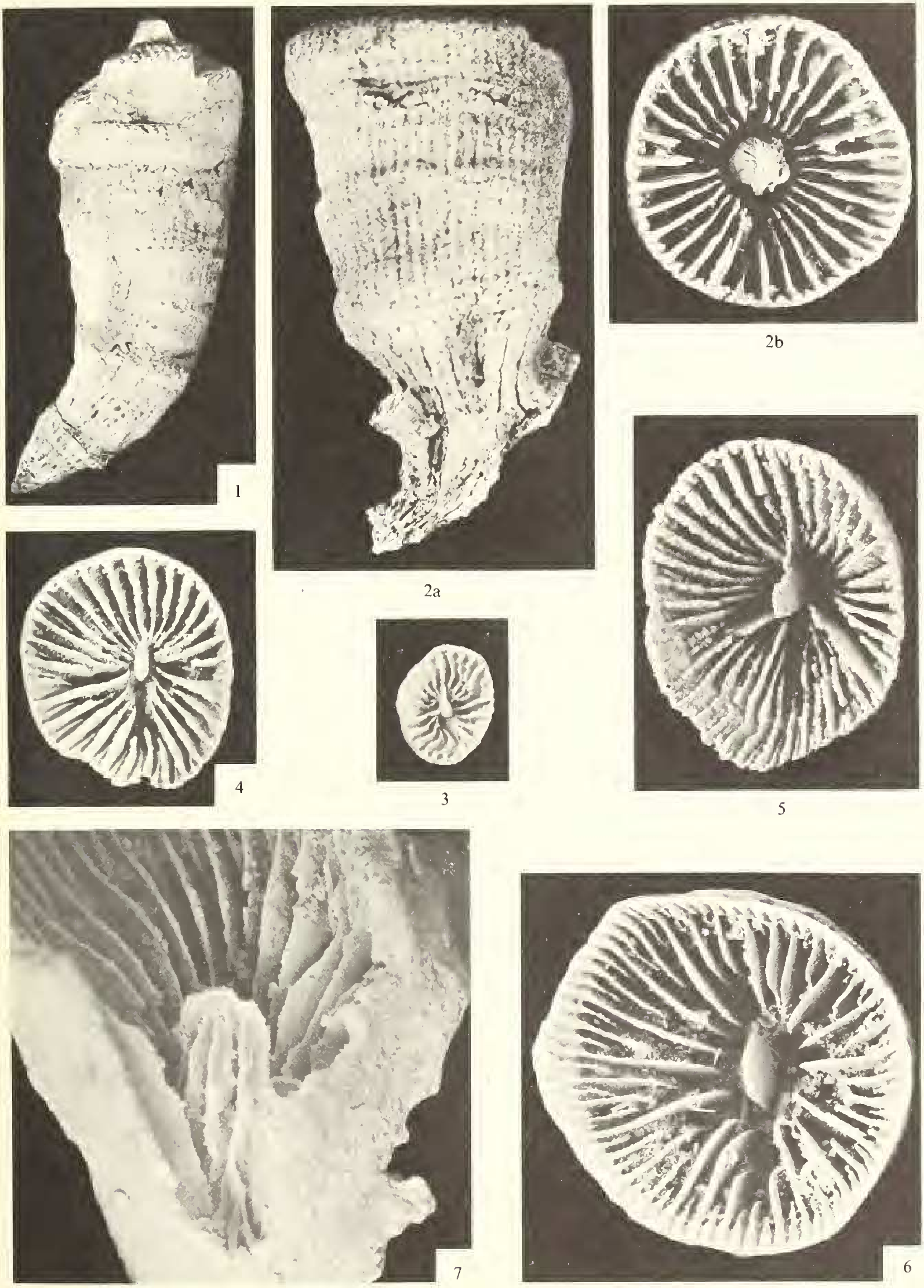
EXPLANATION OF PLATE 60

Fig. 1. *Lophophyllidium proliferum* (McChesney, 1860). Syntype KUM 52878 chosen by Jeffords 1942, ×3.

Fig. 2. *Lophophyllidium* sp. nov. *C*. USNM 189807, Glass Mountains, Texas. Road Canyon Fm., Upper Leonard, ×3.

Figs. 3–6. *Lophophyllidium* sp. nov. *A*. Same locality and age, different stages of growth, ×3. 3, USNM 189808, early neanic stage. Regular arrangement of the major septa. 4, USNM 189809, neanic stage. Regular arrangement of septa. 5, USNM 189810, late neanic stage. Major septa started to be differentiated in length. 6, Holotype USNM 189811, ephebic stage with differentiated length of the major septa.

Fig. 7. *Lophophyllidium* sp. USNM 189812. Same locality and age. Specimen without tabulae. Continuation from the major septa into septal lamellae and outstanding ridge of median lamella on the top of the pseudocolumella is visible, ×5.



FEDOROWSKI, *Lophophyllidium*

structures. Huang (1932) proposed to use the name *Sinophyllum* as a subgenus of *Lophophyllum*, while Wang (1947) synonymized *Sinophyllum* with *Lophophyllidium*. Schouppé and Stacul (1955) discussed the structure of the genera *Lophophyllidium* and *Sinophyllum*, but made no final decision on their relationships. They used the name *Lophophyllidium* and also gave a list of synonyms of the genus *Sinophyllum*. Some authors (e.g. Jeffords 1942, 1947; Wang 1947, 1950; Minato 1955) thought *Sinophyllum* to be a junior synonym of *Lophophyllidium*, while others separated the two genera (e.g. Fontaine 1961; Pyzhjanov 1966). A strange concept of the genera *Lophophyllum*, *Lophophyllidium*, and *Sinophyllum* given by Heritsch (1936) was critically discussed by Fomitshev (1953*a*) and Schouppé and Stacul (1955). The structure of the pseudocolumella interpreted by Fontaine (1961) is the only qualitative difference between *Sinophyllum* and *Lophophyllidium*. The interpretation of Fontaine (1961) differs, however, from that given originally by Grabau (1928). The great variability of this structure found in American specimens suggests that both of these interpretations are valid, but that they do not have taxonomic importance. This variability will be discussed below.

Flügel (1972) introduced a new concept of the family Timorphyllidae Soshkina, 1941. According to him, this family can be divided in two subfamilies: Timorphyllinae and Lophophyllidiinae. The structure of the pseudocolumella, with septal lamellae in Lophophyllidinae and without them in Timorphyllinae, is the only difference between them. Flügel (1972) also synonymized *Stereostylus* with *Sinophyllum* and assigned *Sinophyllum* to the Timorphyllinae. The author agrees neither with Flügel's (1972) family concept nor with the assignment of *Sinophyllum* (= *Lophophyllidium* according to the author) to Timorphyllinae. The structure of the pseudocolumella in both groups of corals is variable and the ontogeny, as well as the microstructure, is different. These similarities and differences between Timorphyllidae and Lophophyllidiidae will be discussed below.

Malonophyllum Okulitch and Albritton, 1937 (type species: *M. texanum* Okulitch and Albritton, 1937). This genus, originally inadequately described and illustrated, was discussed by Moore and Jeffords (1941), who described the second species of this genus, *M. kansasense* Moore and Jeffords, 1941. Lack of tabulae is the only difference between *Malonophyllum* and *Lophophyllidium*. Unfortunately all of Okulitch and Albritton's original material is lost. The originals of *M. kansasense*, re-examined by the present writer, do not seem to have tabulae, even in the proximal ends of corallites, but the preservation of the specimens and their small number (three only) are not adequate to be sure of this feature. It must be emphasized also that there are laminae in the pseudocolumella very similar to those made by tabellae or tabulae in other specimens (Pl. 64, fig. 2). The genus *Malonophyllum* is not accepted by any authors except Moore and Jeffords (1941). It was included in the synonymy of *Lophophyllidium* by Wang (1947, 1950), Hill (1956), and others but none of these authors have restudied either the originals of Okulitch and Albritton (1937) or of Moore and Jeffords (1941).

Soshkineophyllum mirabile Moore and Jeffords, 1941 was included by Jeffords (1947, p. 40) in the synonymy of *Stereostylus*. The original material has been restudied by the present writer and is here synonymized with *Lophophyllidium*.

Stereostylus Jeffords, 1947 (type species: *S. lenis* Jeffords, 1947). The type specimen and some of the

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EXPLANATION OF PLATE 61

Figs. 1, 2. *Lophophyllidium* sp. nov. *D*. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. Relationship between septal lamellae and axial tabellae in pseudocolumella. 1, USNM 189813. Septa are continued on surface of tabella as distinct ridges. No interruption between free tabella and pseudocolumellar lamina is observed, ×5. 2, USNM 189814. Septal lamellae increased as a twisted fold of tabella. Their connections with particular septa are not distinct. Continuation of basal elements is very clear, ×5.

Fig. 3. *Lophophyllidium* sp. nov. *C*. USNM 189815, neanic stage. Almost all major septa reach the distinct, thick pseudocolumella, which remains simple, ×3.

Fig. 4. *Timorphyllum wanneri* Gerth, 1921. USNM 189816. Basleo, Timor, Middle Permian, ×3. *a*, bottom of the calice, where only major septa are visible. *b*, the surface of the corallite with twice as many grooves as major septa.

Fig. 5. *Timorphyllum wanneri* Gerth, 1921. USNM 189817. Same locality and age. Surface of the corallite without epitheca preserved, ×3.

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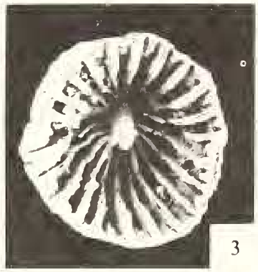

3

4a

4b

5

FEDOROWSKI, *Lophophyllidium* and *Timorphyllum* illustrated specimens are missing. Other illustrated specimens, and quite a few specimens not illustrated, were available for restudy. Ontogeny was almost fully elaborated and illustrated by Jeffords (1947, text-fig. 8). The genus *Stereostylus* was included in the synonymy of *Timorphyllum* by Wang (1947, 1950), but was generally accepted by most later authors, except Duncan (1962) and Rowett and Sutherland (1964), who synonymized it with *Lophophyllidium*, and Flügel (1972) who synonymized it with *Sinophyllum*. According to Jeffords (1947, p. 38), the most important differences between *Stereostylus* and *Lophophyllidium* are: external features of the corallites, smaller apical areas filled by stereoplasm, thinner or more rhopaloid septa, laterally compressed axial column, and lack of radiating and circumscribing laminae in the column. According to Hill (1956), the main character of *Stereostylus* is the pseudocolumella, which is free of the counter septum in the mature stage.

Agarikophyllum Fomitshev, 1953, subgenus of *Lophophyllidium* Grabau, 1928 (type species: *A. pavlovi* Fomitshev, 1953). This subgenus was founded on one incomplete specimen. It was cited and accepted in *Osnovy Paleontologii* (1962) only. The septal lamellae are not completely connected to each other and the small open spaces between them in the pseudocolumella in the mature stage are the main characters of this subgenus. The value of these characters will be discussed below.

Khmerophyllum Fontaine, 1961 (type species: *K. cambodgense* Fontaine, 1961). The structure of the pseudocolumella is the main character of *Khmerophyllum*. It is composed of axial lamella not connected directly with the middle dark line of the counter septum and with radially arranged fascicles of calcite fibres. Kato (1963) connected this genus with *Lophophyllidium*. Fontaine (1964) stated, however, that the microstructure of the septa of *Khmerophyllum* is trabecular and connected it (as a subgenus) with *Sinophyllum*. Flügel (1972) synonymized *Khmerophyllum* with *Lophophyllidium*.

Rotiphyllum Ivanovsky, 1967 does not show any of the characters indicated by Hudson, 1942 for this genus. On the contrary, Ivanovsky's specimen has a very well developed, complex pseudocolumella connected with the counter septum, a shortened cardinal septum, and a *Lophophyllidium*-like arrangement of the major septa; these are characteristic of the genus *Lophophyllidium*.

My reasons for placing all of these genera in synonymy with *Lophophyllidium* are discussed in the following sections.

IMPORTANCE OF BIOMETRIC CRITERIA

The relationship between number of septa and corallite diameter is the most popular, and is generally considered the most important, biometric criterion in tetracorals. However, text-fig. 1 shows that this criterion is not very useful in the group of corals discussed. The holotypes of the type species of the discussed 'genera' included in

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EXPLANATION OF PLATE 62

Fig. 1. *Lophophyllidium proliferum* (McChesney, 1860). Syntype KUM 52878, ×3. *a*, transverse section of neanic stage. *b*, transverse section of ephebic stage. *c*, longitudinal section.

Fig. 2. *Lophophyllidium* sp. nov. *C*. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. Marginal part of corallite USNM 189807 showing the absence of minor septa, ×10.

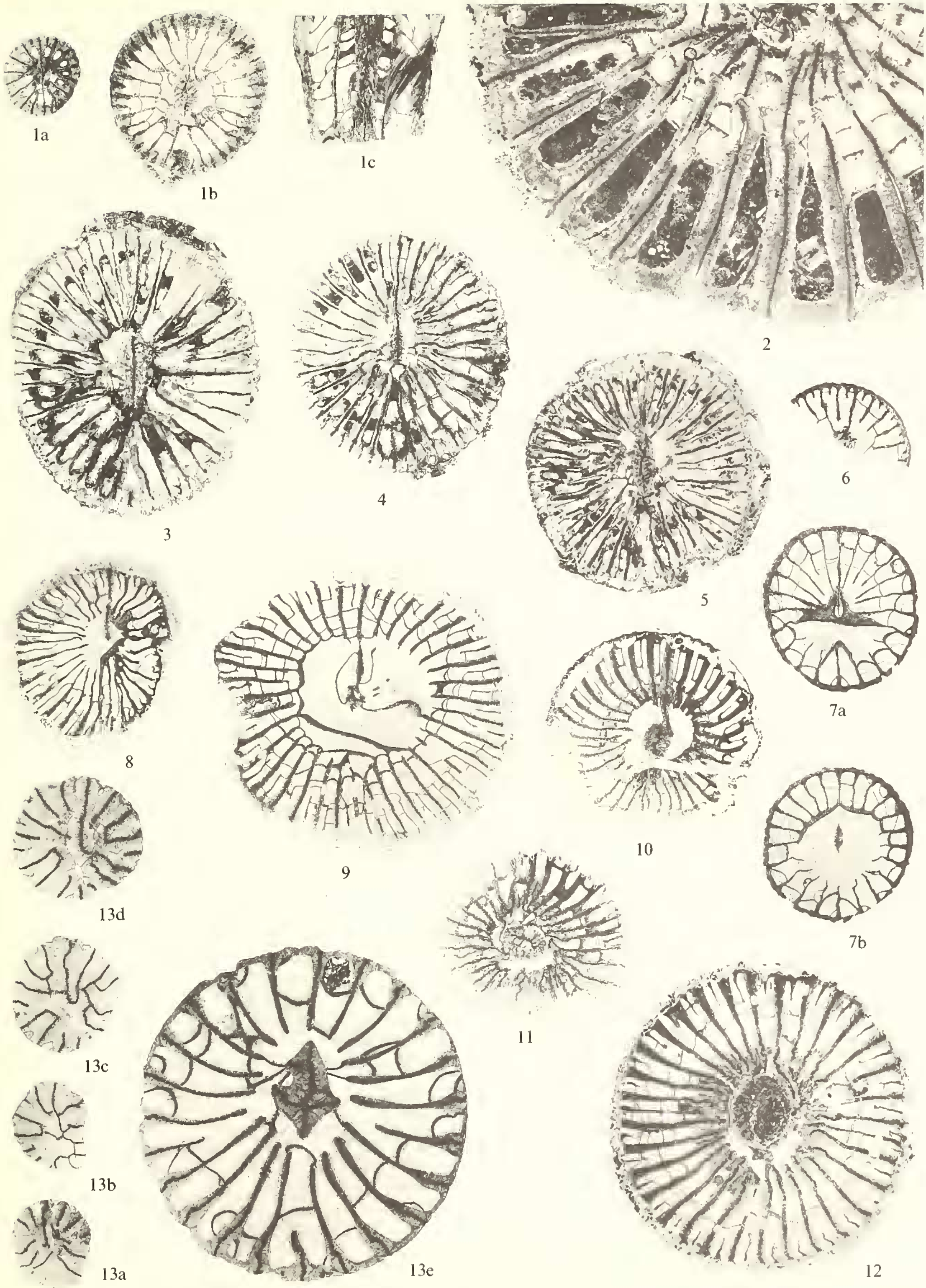
Figs. 3–5. *Lophophyllidium* sp. nov. *A*. Same locality and age. Different stages of development of the contratingent minor septa, ×3. 3, USNM 189818; 4, USNM 189819; 5, USNM 189820.

Fig. 6. *Stereostylus lenis* Jeffords, 1947. Paratype KUM 37361, illustrated by Jeffords (1947, pl. 14, fig. 13*a–c*). Pseudocolumella compound and connected with the counter septum, ×3.

Fig. 7. *Stereostylus lenis* Jeffords, 1947. Paratype KUM 37327. Two successive transverse sections, ×3. *a*, through the tabula with elongated counter septum. *b*, beneath tabula with free pseudocolumella.

Figs. 8–12. *Lophophyllidium* sp. nov. *D*. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. Some examples of the pseudocolumella from simple (fig. 8) to '*Khmerophyllum*'-type (fig. 12), ×3. 8, USNM 189821; 9, USNM 189822; 10, USNM 189823; 11, USNM 189824; 12, USNM 189825.

Fig. 13. *Timorphyllum wanneri* Gerth, 1921. USNM 189826. Basleo, Timor, Middle Permian, ×3. *a–d*, successive transverse sections of neanic stage. Note extremely short cardinal septum. *e*, transverse section of ephebic stage.



FEDOROWSKI, *Lophophyllidium* and *Stereostylus*

Lophophyllidium are marked by capital letters. *Malonophyllum* and *Khmerophyllum* appear to be sharply separated from the others, but it is quite easy to change this impression when some American species, indicated by small letters, are compared. At the same time, these last points are arranged very much like the data of one species only.

Text-fig. 1 does not show the amounts of individual variability of the separate species. It shows, however, that: 1, simple comparison of *n/d* ratio of holotypes or a small number of paratypes is not adequate as a specific character; 2, the *n/d* ratio must be very carefully used, mainly as a secondary rank character; 3, there are some differences among certain groups of species, for example the American and Timor species of *Lophophyllidium*. At the same time the plotted points of Timor *Lophophyllidium* (data after Schouppé and Stacul 1955) show that the Timor specimens of *Timorphyllum* and *Lophophyllidium* are hardly differentiated in the diagram.

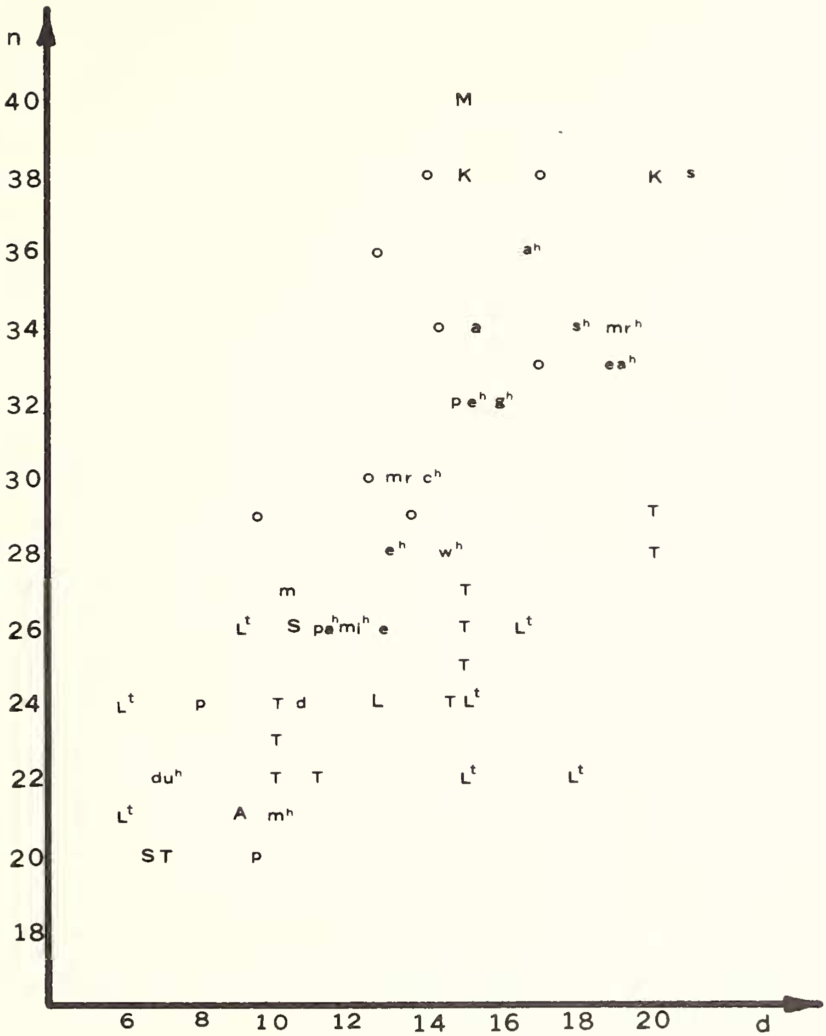
One more observation should be made: the biometric data normally used in literature are mostly accidental. It has not been agreed which part of the corallite should be cut and measured for comparison. Hence, the available data seldom indicate which parts of corallites are compared. Data on the diagram (text-fig. 1) from the holotype of '*Khmerophyllum*' *cambodgense* emphasize how important this is. In fact, it is no less important in most solitary rugose corals. Two regions should be measured and identified: the margin and base of the calice. The measured regions should be indicated.

Other uses of biometry for generic or specific characters (Jeffords 1947), which look quite spectacular, are not meaningful. Relations like length of corallite to its diameter at the calyx and cumulative frequency of length are too closely dependent on the environment to be useful. The length of septa in relation to diameter of corallite (another ratio proposed by Jeffords 1947) has no more importance than the *n/d* ratio, or even less.

ONTOGENY

Fortunately almost all of the discussed genera have juvenile stages more or less completely described. In *Stereostylus lenis* Jeffords (1947, fig. 8) and *Lophophyllidium proliferum* (McChesney 1860) (Duerden 1906) the ontogeny has been investigated from the nepionic (6 septa) stage. *Agarikophyllum* is the only genus in which juvenile stages are unknown.

It is not necessary to redescribe the ontogeny. 1, all the fully investigated specimens have early stages that are typical for the suborder Streptelasmatina—six connected protosepta and paired metasepta in quadrants. 2, arrangement of septa in the early neanic stage is zaphrentoid, with the cardinal and counter septa connected at the corallite axis. 3, counter septum remains elongated and extended to the axial part of corallite while the cardinal septum, which is long during the early part of the neanic stage, becomes gradually shortened in the later part of this stage. 4, axial part of the counter septum may remain simple or some septal lamellae (1–2 or more) may be fused with it making a compound pseudocolumella. 5, in many specimens or species the middle line of the counter septum does not continue into the pseudocolumella, whereas in many others the pseudocolumella becomes free of



TEXT-FIG. 1. Diagram showing the relationship between number of septa (n) and diameter of corallite (d) in holotype specimens of 'genera' synonymized with *Lophophyllidium*, in *Timorphyllum*, and in some American species of *Lophophyllidium*.

A, *Agarikophyllum*; K, *Klmerophyllum*; L, *Lophophyllidium*; L^{t}, *Lophophyllidium* described by Schouppé and Stacul (1955) from Timor; M, *Malophyllum*; S, *Sinophyllum*; ST, *Stereostylus*; T, *Timorphyllum*; O, specimens from Upper Leonard of the Glass Mountains, Texas; a–u, holotypes (with superscript 'h' added) and paratypes of some American species of *Lophophyllidium* described by Moore and Jeffords 1941, 1945 and Jeffords 1942, 1947.

the counter septum in the mature stage; neither the first nor second possibility is connected with a particular pseudocolumella structure. 6, minor septa appear normally very early in ontogeny and are well developed. In some species they appear only in the calice and then disappear into the thick stereoplasmatic layer on the inside surface of the external wall (Pl. 60, fig. 2*b*; Pl. 62, fig. 2).

FINE STRUCTURE

The existence of uni- and multitrabecular fine structure of septa in *Lophophyllidium* was noted by Kato (1963). The arrangement of trabeculae and septal growth lines, however, was not pointed out and illustrated. This structure in one of the original syntypes of *L. proliferum* (McChesney 1860) (Pl. 63, fig. 4), as well as in other American species investigated, should be considered as characteristic for the genus.

Septal growth lines in most of the septa are very steeply, almost vertically arranged. In a few species these lines are almost horizontal in the external part of the septum when the curvature of the upper septal margin is distinctly marked. No septal growth lines running down the external margin of the septum (close to epitheca) were seen.

In longitudinal section, trabeculae are very fine. They intersect mostly two, seldom three or more, septal growth lines. The arrangement of trabeculae is perpendicular to the growth lines. In cross-section they are not distinctly separated from each other and form the structure called lamellar (Schindewolf 1942). No multitrabecular fine structure of septa was found in American specimens investigated. Instead, there are quite a few corals with zigzag structure, which is considered to be a result of recrystallization (see Oekentorp 1972, for discussion).

It is surprising that few of the specimens investigated with the stereoscan microscope have well-organized crystalline structure even when the fine structure in transmitted light is well preserved. Crystals are mostly differentiated into two shapes only: fine crystals in the organic structures of the corallite and larger crystals in the inorganic interspaces. No trabecular arrangement of crystals was found in these septa, presumably a result of recrystallization (Pl. 70, fig. 1). The trabeculae were found in a few other septa, however (Pl. 70, fig. 2). In some parts of the septa the mid-line of the septum can be seen (Pl. 70, fig. 3), but this line is not constant and not visible in every part of the septum. The interruption of the middle line could not be attributed to the trabeculae-like organization of crystals. However, the so-called 'dark

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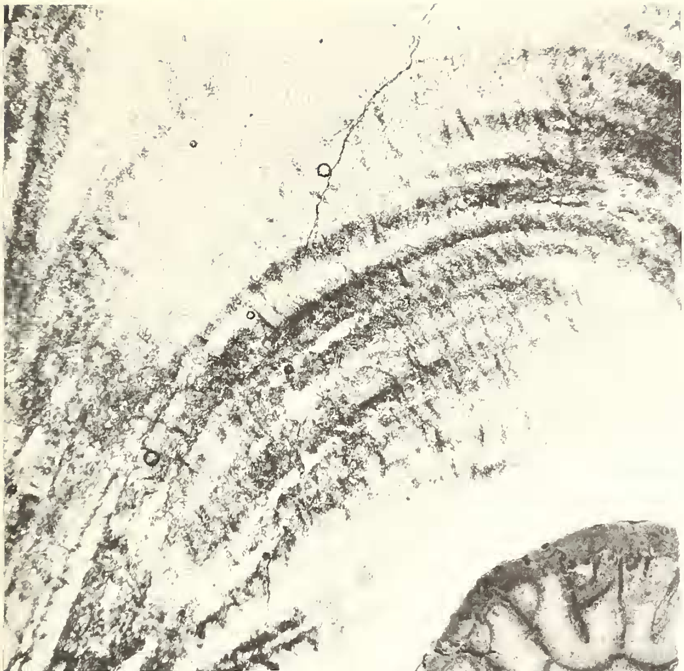
EXPLANATION OF PLATE 63

Fig. 1. *Timorphyllum wanneri* Gerth, 1921. USNM 189827. Basleo, Timor, Middle Permian. Longitudinal section along middle line of septum. External part of corallite on left, × 50.

Fig. 2. *Timorphyllum wanneri* Gerth, 1921. Same specimen, × 3. *a*, *b*, successive transverse sections of the ephebic stage.

Fig. 3. *Lophophyllidium simulans* (Moore and Jeffords, 1941). Holotype KUM 52869. Glass Mountains, Texas. Leonard. Distinct minor septa are visible, × 10.

Figs. 4, 5. *Lophophyllidium proliferum* (McChesney, 1860). Syntype KUM 52878. 4, longitudinal section along septum. External part of corallite on left, × 50. 5, complex structure of pseudocolumella, × 30.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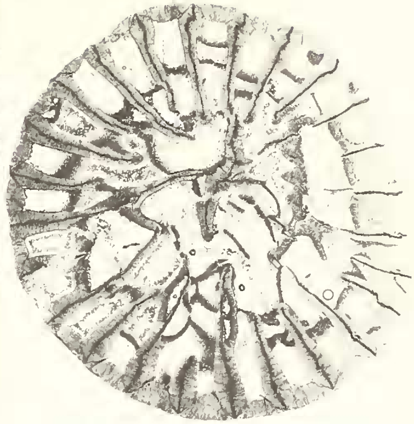
2a


3


2b


4


5

FEDOROWSKI, *Timorphyllum* and *Lophophophyllidium* line' visible in transmitted light is, apparently, the result of the vertical arrangement of crystals in this part of the septum.

I do not agree with Schindewolf's (1942) interpretation of the fine structure of some septa. Since lamellar structure was indicated by Schouppé and Stacul (1955) for *Lophophyllidium* and *Timorphyllum* it should be discussed here. Schindewolf's specimens were not studied and so it cannot be stated definitely that the whole concept of lamellar structure is wrong. It is wrong, however, so far as *Lophophyllidium* and *Timorphyllum* are concerned and those Polycoelaceae studied by Ilina (1965), who identified trabecular microstructure in her specimens.

The transverse section is not the best way to find trabeculae in corals. The longitudinal section made correctly through the middle part of the septum is the only one that can show the presence or absence of trabeculae. Sectioning specimens of *Lophophyllidium* and *Timorphyllum* showed trabeculae in both (Pl. 63, figs. 1, 4). The septal growth lines are shown in the same picture. In my opinion the arrangement of those lines and the arrangement of trabeculae are diagnostic characters for the discussed genera.

Schindewolf's (1942, text-fig. 6 and text-fig. 2*a* herein) original picture was changed slightly by Schouppé and Stacul (1955, text-fig. 9 and text-fig. 2*b* herein), making the interpretation of the real architecture more difficult. It is clear in both of those pictures, however, that the sections of the septum were cut improperly, not perpendicular to the trabeculae (text-fig. 2*c*, line *A'B'*), but perpendicular to the septum (text-fig. 2*c*, line *AB*). As a result of this incorrect angle, the structure visible in the section is misleading (text-fig. 2*d*, *e*). Fibres on one side of the trabecula are cut more or less perpendicular to their crystal axes, while on the opposite side the cut is made almost parallel to the axes. Transmitted light going through the thin section is much more absorbed by fibres cut perpendicularly and one can see the fascicles of fibres shown by Schindewolf (1942) as a lamina. This is especially clear in the case when the trabeculae are slightly flattened (text-fig. 2*d*, *e*). The real architecture is also obscured by secondary septal accretion, which is often a continuation of the primary septal deposits. The internal margin of the septum, where the growth lines are almost vertical and trabeculae almost horizontal, is the best place to demonstrate what was stated above. There the points of the septal trabeculae are cut very obliquely and therefore the 'laminae' are very distinct. In *Timorphyllum*, where the growth lines of the septa are convex in the middle part, one can observe the 'laminae' in the external,

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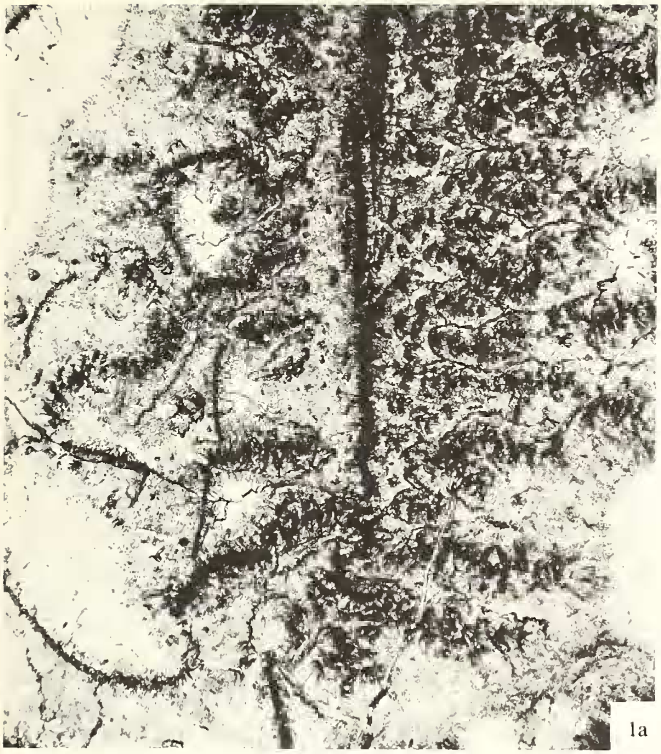
EXPLANATION OF PLATE 64

All figures ×30.

Fig. 1. *Lophophyllidium* sp. nov. *A*. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. USNM 189828. Three successive transverse sections of the pseudocolumella beneath the bottom of the calice. *a*, complex, mostly septo-lamellar pseudocolumella. *b*, septo-lamellar structure in internal part and tabulo-laminar structure in external part of pseudocolumella. *c*, tabulo-laminar part of pseudocolumella.

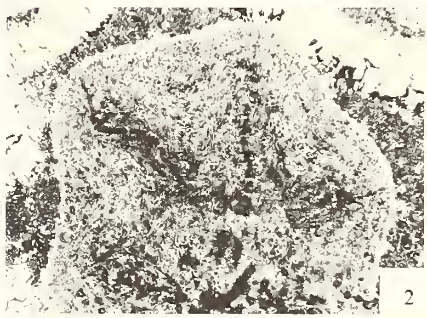
Fig. 2. *Malonophyllum kansasense* Moore and Jeffords, 1942. Holotype KUM 52848. Part of pseudocolumella with weakly septo-lamellar structure filled up secondarily by tabulo (?)-laminae.

Fig. 3. *Lophophyllidium* sp. nov. *D*. USNM 189822. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. Weak, small, complex pseudocolumella.


1a


1c


1b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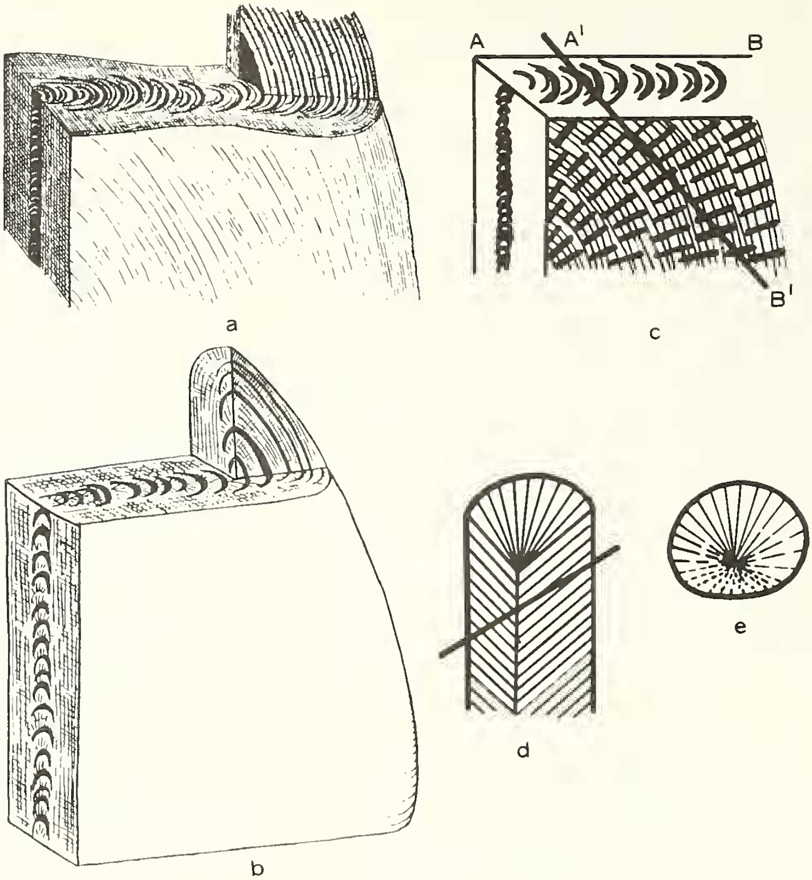
FEDOROWSKI, *Lophophyllidium* and *Malonophyllum*



TEXT-FIG. 2. Interpretation of lamellar fine structure of septa.
a, Schindewolf's (1942) schematic picture.
b, Schouppé and Stacul's (1955) modification of the previous picture.
c, author's interpretation of Schindewolf's (1942) picture with trabeculae perpendicular to the growth lines. *A–B* section given by Schindewolf is very oblique to trabeculae. *A′–B′* section more or less perpendicular to the trabeculae.
d, supposed irregular trabecula with the line of section given obliquely.
e, the same trabecula cut along the oblique plane showing in *d*.

EXPLANATION OF PLATE 65

Fig. 1. *Lophophyllidium extumidum* Moore and Jeffords, 1945. Paratype USNM 140325 (figured by Moore and Jeffords, 1945, fig. 21*a*, *b*), ×30. *a*, transverse section of pseudocolumella. *b*, longitudinal section between septa showing connection of free tabellae and pseudocolumellar laminae.

Fig. 2. *Lophophyllidium extumidum* Moore and Jeffords, 1945. Paratype USNM 140324 (figured by Moore and Jeffords 1945, fig. 17*a–c*), ×50. Longitudinal section along septum and through pseudocolumella, showing connections between growth lines of septum and pseudocolumella.

Fig. 3. *Lophophyllidium hadrum* Jeffords, 1947. Holotype KUM 32279 (figured by Jeffords 1947, pl. 3, fig. 3*a–d*. Compare also Pl. 67, fig. 3 in this paper). Complex and compact pseudocolumella in the neanic stage of corallite, ×30.

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FEDOROWSKI, *Lophophyllidium*

as well as in the internal, part of the septum, although oppositely directed (Pl. 66, fig. 3), and there are no 'laminae' at all in the more perpendicularly cut, middle part of the septum.

MACROSTRUCTURES

Major septa

Major septa are not very important systematically in the genera discussed, in contrast to their usefulness in many other groups of corals. The arrangement of septa in the young stage is similar in all synonymized genera, as discussed above. Arrangement in the mature stage varies from pinnate through bilateral to radial in the species investigated. At the same time, the length of particular septa in cross-section and in the calice can be changeable. The cardinal septum is generally shortened, but can be almost as long as the rest of the major septa in some species. In this case, however, the last pair of metasepta in the cardinal quadrants is generally shortened. Alar septa in many described species are slightly or much elongated. There are many other species in which these septa are equal in length to other major septa and can be distinguished only by the presence of the last pair of shortened metasepta in the counter quadrants as seen in cross-section or on the surface of the corallite. Alar septa are never shortened. Metasepta may be more or less equal in length in some species, while in other ones they are very much differentiated. This character, as well as the total length of major septa in comparison to the corallite diameter is very often consistent in particular species, but only in comparable growth stages. Changes of arrangement and length of major septa during ontogeny in one species are shown on Plate 60, figs. 3–6. The counter septum will be discussed together with the pseudocolumella.

Minor septa

The minor septa are commonly free and quite short, as illustrated by many authors. It is possible, however, to find among *Lophophyllidium* species, quite different types:

1. Underdeveloped minor septa, which are characteristic, for example, of *Lophophyllidium* sp. nov. *C*. They are quite visible in the calices and more or less (Pl. 60, fig. 2*a*, *b*) on the surface of corallites, but they are completely covered by stereoplasm beginning from half the depth of calices down. No minor septa are visible in cross-sections of the specimens of this species (Pl. 62, fig. 2), except in sections through the uppermost part of the calice.

2. Completely or partly contratingent minor septa. It is not clear which kind of minor septa should be called contratingent, those with dark lines of major and minor septa fused or those in which only the light tissue is in contact. Only the second case

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EXPLANATION OF PLATE 66

Fig. 1. *Lophophyllidium* sp. nov. *A*. USNM 189829. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. Longitudinal section along tabello-lamellar pseudocolumella, ×30.

Figs. 2, 3. *Timorphyllum wanneri* Gerth, 1921. USNM 189826. Basleo, Timor, Middle Permian. 2, SEM photomicrograph of zigzag arrangement of trabeculae, ×350. 3, transverse section of septum (a piece of middle part of septum was cut out) showing 'lamellar' structure both in external (down) and internal part of septum and the zigzag arrangement of the trabeculae in its middle part, ×50.

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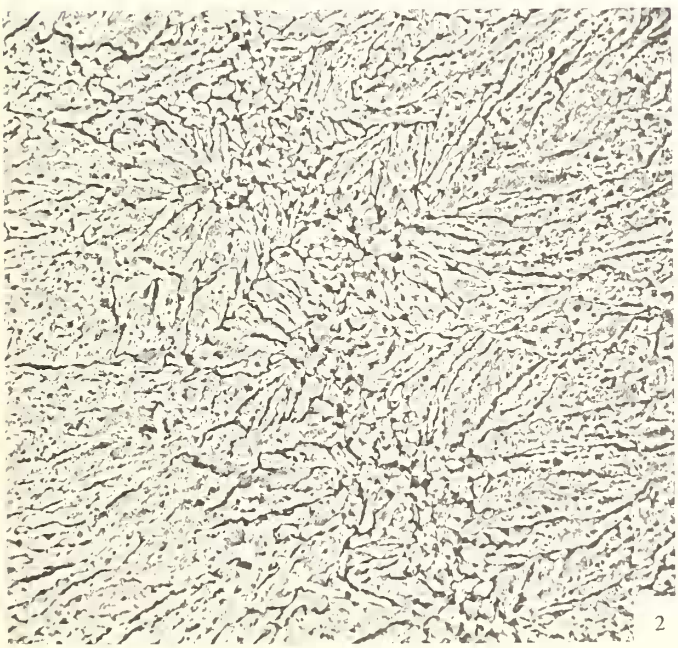

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FEDOROWSKI, *Lophophyllidium* and *Timorphyllum* has been observed in Texas specimens. On Plate 62, figs. 3–5 a few corallites from the same species and locality with normal and contratingent septa are shown. The full intraspecific variability of this character will be discussed and illustrated in a future paper. Of course, as in every case of contratingency, the triad at the counter septum is developed.

Pseudocolumella

This is the structure on which most speculations about this group of corals have been based. It is closely related to the counter septum in all of the discussed genera. It may be separated from the axial end of the counter septum or be permanently a part of it. The pseudocolumella is monoseptal in all neanic stages studied. Beginning from the late neanic stage there are several types of gradual change, most of which were considered typical for particular genera: simple pseudocolumella, which can be free of the counter septum; in *Stereostylus*, pseudocolumella composed of septal lamellae, in *Lophophyllidium*; pseudocolumella, pendulum-like, composed of fibres (according to Fontaine 1961; *non* Grabau 1928), in *Sinophyllum*; pseudocolumella composed of radially arranged fascicles of fibres, in *Khmerophyllum*; pseudocolumella with septal lamellae not closely packed, in *Agarikophyllum*; pseudocolumella 'concentrically lamellar' (Okulich and Albritton 1937) or composed of septal lamellae and layers of stereoplasm (in Moore and Jeffords' revised specimens), in *Malonophyllum*.

The following observations resulting from a study of North American specimens can be easily transferred to the type specimens of the discussed 'genera'.

Simple pseudocolumella. This is typically developed in the juvenile stages of all specimens in this group of corals, but can remain unchanged to the end of ontogeny. It can be built as a simple elongation of the counter septum, sometimes not even thickened (Pl. 60, fig. 5; Pl. 62, fig. 8) or with stereoplasmatic covers (Pl. 61, fig. 3; Pl. 62, fig. 7*a*). It can also be completely free of the counter septum (Pl. 62, fig. 7*b*). The successive stages of the process of its separation will be discussed below.

The young corallites are the best proof that the pseudocolumella can be very distinct and stereoplasmatically thickened, remaining monoseptal at the same time. It is true even in specimens having a composite pseudocolumella in the mature stage (Pl. 61, fig. 3). Many major septa reach the pseudocolumella here, but do not penetrate

EXPLANATION OF PLATE 67

All figures ×30.

Fig. 1. *Lophophyllidium* sp. nov. *B*. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. USNM 189830 showing secondary zigzag fine structure of septa and one of the possibilities of breaking the connection between pseudocolumella and counter septum on the successive transverse sections. *a*, middle line of counter septum (horizontal on the upper part of the picture) is connected at right angles with the middle lamella. *b*, counter septum (vertical, left part of picture) is overpassing pseudocolumella at its side.

Fig. 2. *Lophophyllidium* sp. nov. *D*. USNM 189831. Same locality and age. A few incipient septal lamellae in thin pseudocolumella connected with counter septum.

Fig. 3. *Lophophyllidium hadrum* Jeffords, 1947. Holotype KUM 32279 (compare also Pl. 65, fig. 3 in this paper). Cross-section of the pseudocolumella of the adult part of specimen showing weak, '*Agarikophyllum*'-type structure.

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FEDOROWSKI, *Lophophyllidium*

it. The process of the gradual complication of the structure of the pseudocolumella can be observed both in the ontogeny of the same specimen and as individual variation in different specimens belonging to the same species. *Lophophyllidium* sp. nov. *D* is a good example of the last case (Pl. 62, figs. 8–12). The pseudocolumella changes here from simple to very complex while the other structural elements remain stable and similar.

Composite pseudocolumella. (1) A *lamellar pseudocolumella* is composed of the axial end of the counter septum (medial lamella) and septal lamellae. The medial lamella in well-preserved specimens always rests on the thickened part of the pseudocolumella (Pl. 60, figs. 2*b*, 7). The 'pure' lamellar pseudocolumella can be investigated mainly in the calices of specimens without tabulae. One can see there that the septal lamellae are situated vertically or obliquely on the surface of the medial lamella. They begin to develop close to the upper part of the medial lamella as very tiny folds, which become gradually larger downwards (Pl. 60, fig. 7). Septal lamellae in such specimens are directly fused with major septa at the same level, i.e. the apparent base of the calice. It is the same level, common for each of the major septa, at which their direction of growth changes from being directed into the corallite centre through a short section of upward growth (apparent base of the calice) to growth outwards. The last type of growth is characteristic for septal lamellae. In addition almost all major septa in most of the investigated specimens, turn right (counter-clockwise) on the apparent base of the calice. All the described changes can be observed both in the calice (Pl. 60, fig. 7), and in the transverse section of the columella, where the fascicles of fibres are situated opposite to those in the septa (Pl. 69, fig. 2). Indeed, the septa and septal lamellae cannot be separated from each other. The origin of both is the same. Both are secreted in the same fold of ectoderm, which began at the epitheca and ended close to the top of the pseudocolumella, where it connected with the fold of ectoderm which secreted the medial lamella.

Septal lamellae in specimens without tabulae are usually distinct and clearly separated from each other under the apparent bottom of calice. Beneath it they can be connected to each other if numerous. If there are only a few septal lamellae, the spaces between them are secondarily filled by the stereoplasmatic thickening of the medial lamella. The fine structure of these parts is fibrous, or can be zigzag, when recrystallized (Pl. 69, fig. 1). Between widely separated septal lamellae, however, the

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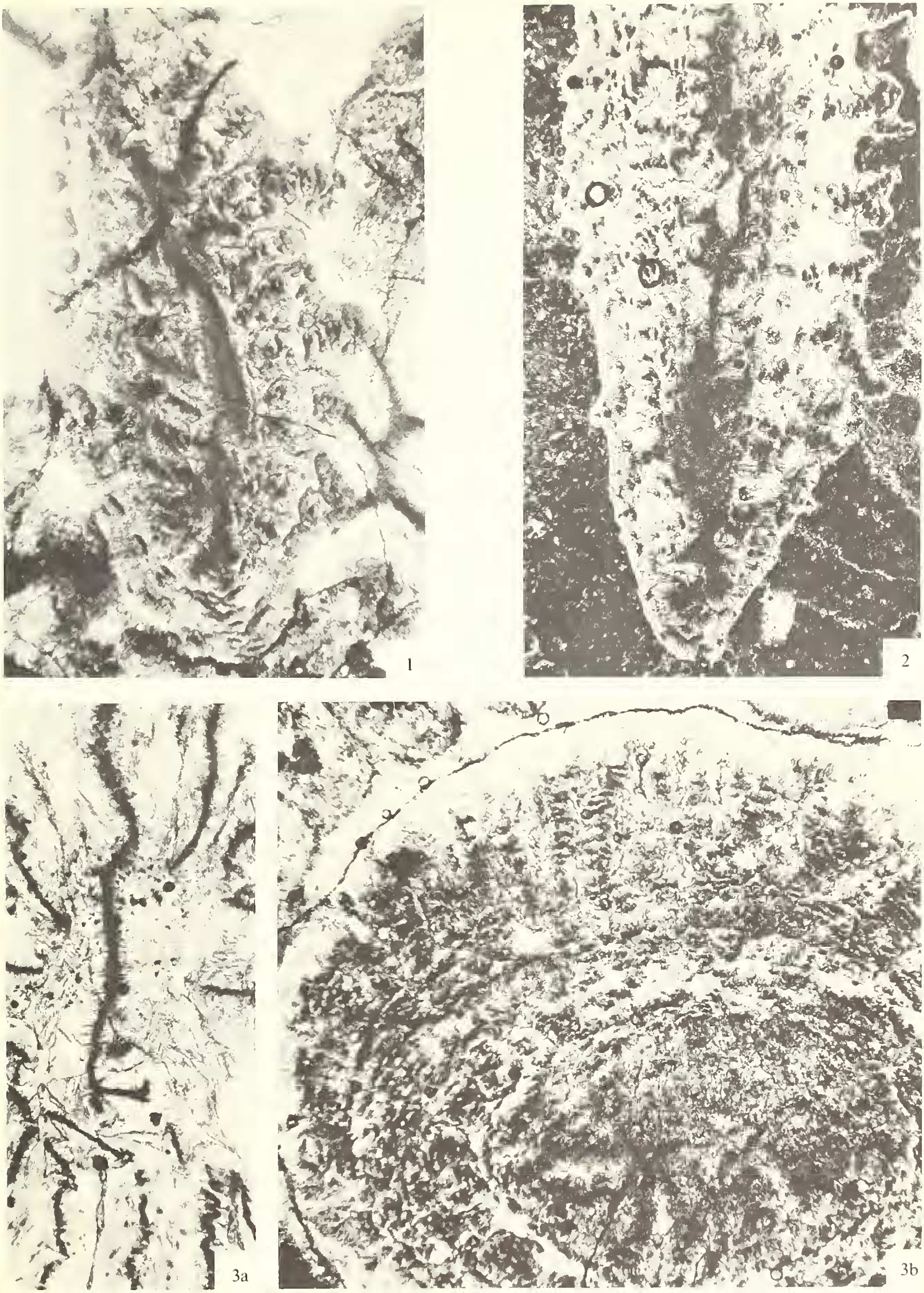
EXPLANATION OF PLATE 68

All figures $\times 30$.

Fig. 1. *Lophophyllidium* sp. nov. *A*. USNM 189832. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. Transverse section of pseudocolumella showing closely packed septal lamellae in the internal part and laminar structure with a few septal lamellae in the left part.

Fig. 2. *Lophophyllidium* sp. nov. *A*. USNM 189829. Same locality and age. Transverse section of the pseudocolumella showing regular, lamello-tabellar structure.

Fig. 3. *Lophophyllidium* sp. nov. *D*. USNM 189825. Same locality and age. *a*, transverse section of pseudocolumella in neanic stage with two septal lamellae only. *b*, transverse section of the pseudocolumella in the adult stage showing '*Khmerophyllum*'-type structure.



FEDOROWSKI, *Lophophyllidium*

axial, steeply arched tabellae commonly penetrate. These tabellae could be elongated without any boundary into the structure of the pseudocolumella. Laminar structure of the pseudocolumella between septal lamellae may be observed in this case (Pl. 68, figs. 1, 2). The latter structure can be called the lamello-tabellar pseudocolumella.

(2) *Lamello-tabellar pseudocolumella.* A pseudocolumella of this type is derived from that mentioned above by a change of rhythm of the secretion of the structural elements. The surfaces of axial tabellae become the bases for septal lamellae (Pl. 61, figs. 1, 2). This change of rhythm can be observed in many cross-sections of the pseudocolumellae (Pl. 68, fig. 3*b*). Many of the intermediate stages observed suggest that this passing from one structure to another was probably not genetically determined and thus not helpful for taxonomic purposes. Most probably this change is a function of time (= stage of growth) and very much dependent on individual variability. There are quite a few corallites in the investigated collection that did not build lamello-tabellar pseudocolumellae. There are also many others in which only very narrow or incomplete parts of laminar structure can be observed; in these cases, growth of lamellae was faster than growth of the basal elements, which did not cover the previous ones (Pl. 69, fig. 2). At least there are such corallites in the collection possessing a pseudocolumella in which axial tabellae predominate, while the lamellae are settled in them as short sparse fascicles or fibres (Pl. 69, fig. 3). A good example of the entire change of the structure of the pseudocolumella in the same specimen is shown on Plate 64, fig. 1*a–c*. The pseudocolumella is monoseptal at the beginning, as in all other specimens of the genus, and then becomes lamellar, lamello-tabellar, and simple-lamellar close to the calice, but still beneath the last tabula.

The lamello-tabellar pseudocolumella can have sometimes a little non-typical structure, which has been interpreted as a generic character (*Agarikophyllum*, *Khmerophyllum*). The pseudocolumella of the *Khmerophyllum*-type appeared when septal lamellae are spirally arranged and very closely packed on the particular tabellae (Pl. 68, fig. 3*b*). The cross-section of such a pseudocolumella characteristically shows more or less regularly arranged fascicles of fibres in a comparatively long row. This occurred when the septal pockets of ectoderm on the successive tabellae increased immediately one after another. The degree of complication of this type of pseudocolumella can be very great. In one Glass Mountains species, very great variability of this character was noted, and three extreme forms of pseudocolumella for this species are illustrated (Pl. 64, fig. 3; Pl. 67, fig. 2; Pl. 68, fig. 3*a*, *b*).

The pseudocolumella of the *Agarikophyllum*-type appears in specimens which do not have thick, secondarily secreted stereoplasmatic sheets on the primary structural

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EXPLANATION OF PLATE 69

All figures ×30.

Figs. 1–3. *Lophophyllidium* sp. nov. *A*. Glass Mountains, Texas. Road Canyon Fm., Upper Leonard. 1, USNM 189833 showing middle line of counter septum just after interruption of the middle line of pseudocolumella. Septal lamellae rarely placed, with laminar (recrystallized in zigzag structure) layers between them. 2, USNM 189834. Pseudocolumella free of counter septum is built by closely packed septal lamellae. 3, USNM 189835. Middle line of counter septum is connected with median lamella. Pseudocolumella mostly lamellar with rarely arranged, short, fascicle-like septal lamellae.

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FEDOROWSKI, *Lophophyllidium*

elements. It can be observed mostly just before the end of the individual development. *Lophophyllidium hadrum* Jeffords (Pl. 65, fig. 3; Pl. 67, fig. 3) is a good example of this kind of structure. The normal, closely packed lamello-tabellar pseudocolumella starts to weaken inside the calice region, without losing its primary external shape. This type of pseudocolumella should be considered as a gerontic, or at most, a specific character.

Explanation of some of the terms used in this discussion. 1. 'Lamellae increasing on the surface of the tabellae' can be taken literally when the new septal lamella appears after a separate period of only tabellar (laminar) secretion. This happens quite often, but not so generally as the second possibility, i.e. when both of the secretions, tabellar and lamellar, are practically contemporary. In the last case, ectodermal pockets secreting septal lamellae are formed after a very short period of flat, tabular secretion or even without it in some places. It can be observed in longitudinal section, when pieces of lamellae, intersecting a few tabellae are visible. It is difficult to distinguish the axial tabellae in cross-section, when septal lamellae are very closely packed; it is almost always possible in the longitudinal section, however (Pl. 66, fig. 1).

2. The term 'lamello-tabellar pseudocolumella' could be restricted. It is difficult to identify with certainty the laminae with the axial tabellae in the pseudocolumella. In longitudinal sections of many corallites one can observe the continuation from free tabella into pseudocolumellar lamina (Pl. 65, fig. 1*a*). In other corallites or in particular parts of them, however, only tabellae seem to reach the pseudocolumella. It is almost impossible to distinguish particular laminae in the pseudocolumella in these sectors of the pseudocolumella, but it is still possible in others. The analysis of quite a few specimens assured the author that both of the basal elements—free axial tabellae or tabulae and pseudocolumellar laminae—were secreted contemporaneously by continuous basal ectoderm.

Concerning the relationship between septal lamellae and pseudocolumellar laminae, *Lophophyllidium extumidum* Moore and Jeffords, 1945 gives more information. The pseudocolumella in cross-section of this species appears to be laminar only (Pl. 65, fig. 1*a*). In longitudinal section, however (in the section made between septa) (Pl. 65, fig. 1*b*), the continuation from free tabula into pseudocolumellar lamina is visible, and in section made along the septum, close to its middle line, the growth lines of the septum are continued right up into the growth lines of the pseudocolumella (Pl. 65, fig. 2). The described example proves the uniformity and replacement of such seemingly different structures as septal lamellae and axial tabellae (or pseudocolumellar laminae) in the pseudocolumella.

The connection of the counter septum and pseudocolumella may be complete or only apparent. Many pseudocolumellae are isolated. Full connection occurs when the mid-line of the counter septum is continued into the mid-line of the pseudo-

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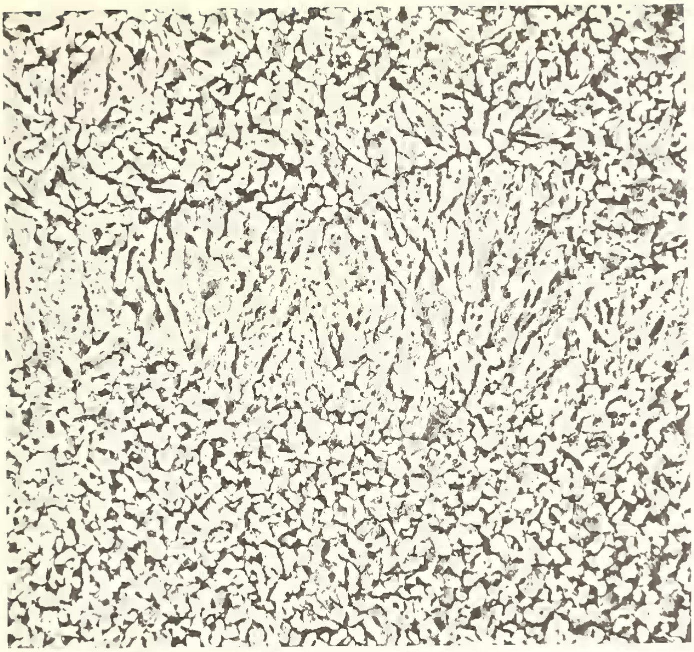
EXPLANATION OF PLATE 70

All figures ×500.

Fig. 1. *Timorphyllum wanneri* Gerth, 1921. USNM 189826. SEM micrograph of longitudinal section of tabula (photo W. R. Brown).

Figs. 2–4. *Lophophyllidium* sp. nov. *A*. SEM micrograph of transverse sections of septa. 2, USNM 189811. Two very small trabeculae in the middle part of septum (photo Dr. J. E. Sorauf). 3, USNM 189828. Primary septal structure (dark middle line in transmitted light) is visible as small crystals with apparent random arrangement. The big crystals at the margins are secondary organic septal structure. Both structures are changed by recrystallization. 4, USNM 189836. Secondary zigzag structure due to recrystallization of mid part of septum. Long crystals preserved in some places may be remnants of particular trabeculae.



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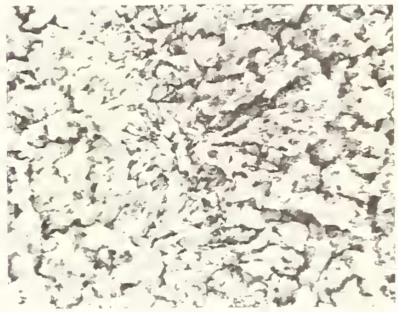

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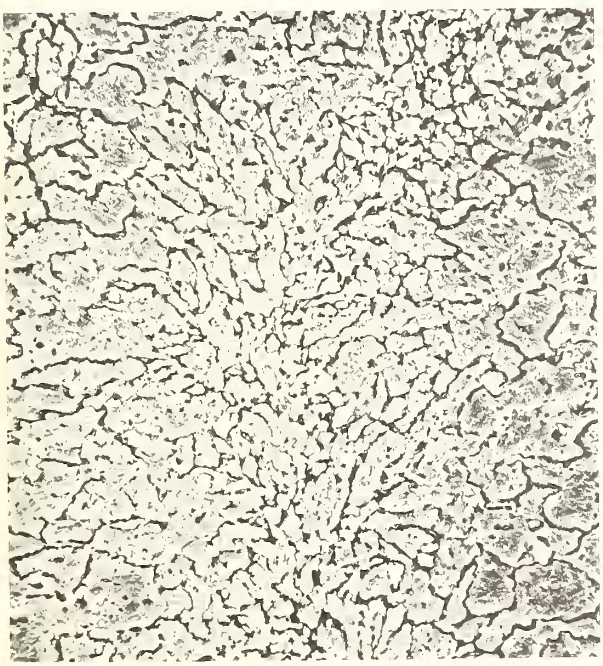

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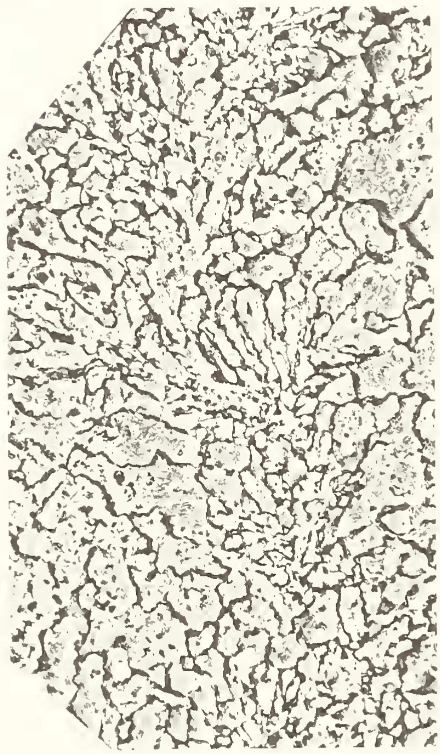

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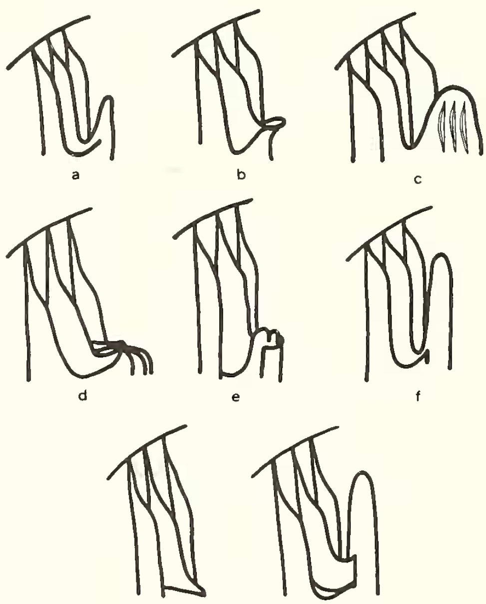
FEDOROWSKI, *Timorphyllum* and *Lophophyllidium* columella. Apparent connection occurs when the mid-lines are not fused or when the side of the counter septum rests against the pseudocolumella. The complete isolation of the pseudocolumella and counter septum is produced either by shortening of the counter septum or by change of direction of its growth; it can be parallel to the pseudocolumella without any connection with it. On Plate 67, fig. 1*a*, *b* and Plate 69, figs. 1, 3 a few successive stages of the relationship between those two elements are shown. This character is not of great value for systematics even at the specific level.

The shape of the counter septum in the calice and its connection with the pseudo-columella in this part of the corallite may have some value for specific identification. However, this character must be very carefully investigated both in ontogeny and individual variability before using it for this purpose. Some examples of shapes of the counter septum are shown on text-fig. 3.



TEXT-FIG. 3. Different shape of counter septa and different kinds of connections with pseudocolumellae in species of *Lophophyllidium* from Glass Mountains, Texas (Leonardian).

a–c, *Lophophyllidium* sp. nov. *A*; counter septum and pseudocolumella in the specimens are in different stages of growth.

d, *e*, *Lophophyllidium* sp. nov. *B*; different shape of septa and pseudocolumellae in mature specimens.

f, *Lophophyllidium* sp. nov. *C*; typical relationship between septa and pseudocolumella.

g, *h*, *Lophophyllidium* sp. nov. *D*; different shape of septa and pseudocolumella in mature specimens.

Tabularium

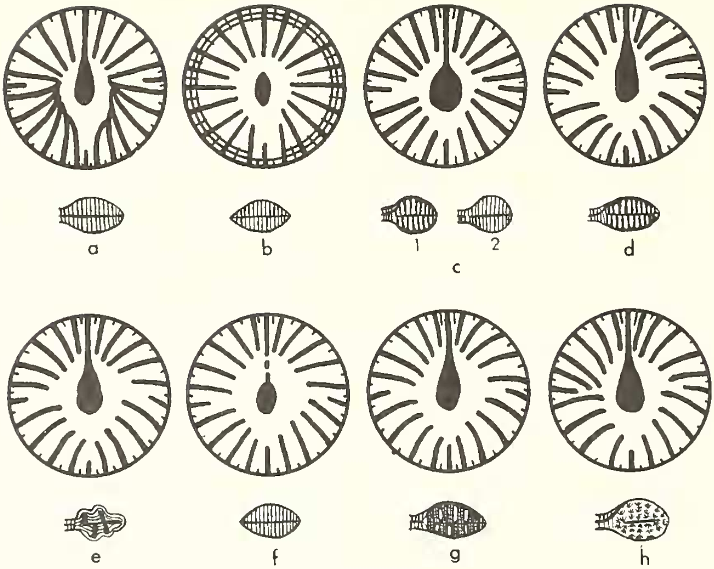
Among the corals assigned by the author to *Lophophyllidium* are many individuals without a tabularium, i.e. without tabulae. All appear to have juvenile characters: pinnate arrangement of septa which reach a simple, not compound pseudocolumella. It is possible to arrange these specimens in a limited development line and compare them with the stages of mature specimens which do possess a tabularium.

Arrangement and number of septa in both groups are approximately the same (septa were numbered on the apparent bottom of calices) when individual variability is considered. The cross-sections of young stages of mature specimens differ from the young corallites without tabularia in having thick, secondary stereoplasmatic sheets on the septa. The moment when the corallite started to secrete tabulae is very variable in this group of corals, but it happened mostly late in ontogeny. It seems that tabulae are not very important skeletal elements here. The apparent bottom of the calice, as well as the strong skeleton in the central part of corallite (pseudocolumella in calice and stereoplasmatic column beneath it), make the tabulae unimportant from a mechanical point of view. The secreted vertical elements were probably sufficient both for supporting the body of the polyp and for protecting the corallite against external pressure.

No mature individuals without a tabularium were found among the corals studied by the author. It seems, however, that three specimens from Kansas described by Moore and Jeffords (1941) as *Malonophyllum kansasense*, have no tabularium even in the mature (or mature-like) stage. However, they have laminae in the pseudocolumella (Pl. 64, fig. 2). It is not considered in this particular case that the lack of a tabulae is an adequate generic character, because of the poor preservation of the Kansas material, as well as wide heterochronism observed among very similar corals. *Malonophyllum* and *Lophophyllidium* are therefore considered synonyms.

STRATIGRAPHIC POSITION

Reports of species of the discussed genera in the Lower Carboniferous are very sporadic and poor. Vojnovsky-Krieger (1934) described one incomplete specimen from the Gornyi Altai as *Lophophyllum micula*. The original material in the Tschernyshev Museum in Leningrad has been examined. It has a well-developed counter septum and a kind of pseudocolumella, but its very short septa and flat tabulae can hardly be compared with those of *Lophophyllidium proliferum*. The possibility of some relationship with *Lophophyllidium* cannot be excluded. Stuckenberg (1904) described *Lophophyllum minimum*, which may be a representative of the genus *Lophophyllidium*, but it may actually belong to *Lophophyllum* or be a young corallite (without dissepimentarium) of *Koninckophyllum*. The material in Leningrad consists of three pieces of corallite sectioned transversely and obliquely. In transverse section the septa are thin and uniform, except for a shortened cardinal and elongated counter septa. The pseudocolumella is well developed, not compound; quite a few sectioned tabellae surround it. In oblique section, arched tabulae and a well-developed pseudocolumella are visible. The material is not adequate to make a final decision about its generic position. Stuckenberg's stratigraphic designation (Lower Carboniferous) is also not certain.



TEXT-FIG. 4. Schematic drawings showing arrangement of septa and structure of pseudocolumella in particular genera synonymized in the paper.

a, *Lophophyllum* Milne-Edwards and Haime according to Lecompte (1955) revision based on type material (type species *Lophophyllum konincki* Milne-Edwards and Haime). Keyhole cardinal fossula and simple columella.

b, *Lophophyllum* Milne-Edwards and Haime according to Carruthers (1913) revision based on topotype material (type species *Cyathaxonia tortuosa* Michelin). Specimens possess dissepimentarium and simple columella. They were later synonymized with *Koninckophyllum* Nicholson and Thomson, 1876.

c, *Sinophyllum* Grabau, 1928. *c* 1, pseudocolumella according to Grabau, 1928 possesses a 'series of rod-shaped bodies' which were compared by Huang (1932) and Wang (1947) with the septal lamellae of *Lophophyllidium proliferum*. *c* 2, pseudocolumella built with simple fibres of calcite, according to Fontaine 1961.

d, *Lophophyllidium* and the next four 'genera' have the same arrangement of major septa with shortened cardinal septum, elongated counter septum, and more or less distinct pseudofossulae. *Lophophyllidium* has pseudocolumella complex, built with septal lamellae.

e, *Malonophyllum*, pseudocolumella built with rare septal lamellae and probably tabular laminae. According to Okulitch and Albritton 1937 there are no tabulae.

f, *Stereostylus*, pseudocolumella may be connected with counter septum or free of it. It may also be simple or complex in the different paratypes of the type species.

g, *Agarikophyllum*, pseudocolumella not completely compact. Particular septal lamellae may not be connected with each other.

h, *Khmerophyllum*, pseudocolumella built with short fascicles of calcite situated on the tabular laminae.

Rotiphyllum sp. described by Ivanovsky (1967) from the Lower Carboniferous (Lower Miksin stage) of the Lena River seems to be definitely a representative of the genus *Lophophyllidium* with a compound pseudocolumella. This, and *Lophophyllidium* sp. described by Kostic-Podgorska (1955) from the Lower Carboniferous of Yugoslavia are presently the best illustrated and most definite representatives of *Lophophyllidium* from the Lower Carboniferous.

Termier and Termier (1950) reported *Stereostylus* and a few other similar forms from the Viséan and probably Namurian of Morocco. Among them, some cross-sections of *Stereostylus maroccanus* (Termier and Termier 1950, pl. 35, fig. 28) look similar to normally developed *Lophophyllidium* species, despite Termier and Termier having stated that a dissepimentarium is present. The dissepiment-like structures look very similar to sections of the external parts of tabulae. This specimen was described from the Viséan/Namurian boundary. In the same paper Termier and Termier illustrated some other *Lophophyllidium*-like specimens, *Cyathaxonia* sp. (pl. 36, fig. 5) from the Viséan and *Cyathaxonia* (?) sp. (pl. 36, fig. 21) from uppermost Viséan or Namurian. All these specimens may belong to the genus *Rylstonia* or to *Lophophyllidium*. The material has not been seen and no longitudinal sections were illustrated. Drawings made by Termier and Termier are inadequate.

There are no reports of any *Lophophyllidium*-like corals from the Lower and Middle Namurian. However, the coral fauna of that age is one of the poorest known from the Carboniferous.

Corals of *Lophophyllidium* and *Stereostylus* type became quite common in the Lower Morrowan (Namurian C) of the U.S.A. (Jeffords 1942; Moore and Jeffords 1945; Rowett and Sutherland 1964), but they are not recorded from Europe or Asia. Dr. N. P. Vassiljuk kindly informed the author (written communication 1973) that she has one specimen of *Lophophyllidium* from Namurian C (Limestone F_2^1) of the Donets Basin and that there are some *Lophophyllidium* corals in the Bashkirian of the Petshora region and in the Moskovian of the North Ural. Fomitshev's (1953*a*) paper is the first report of *Lophophyllidium* in Westphalian A (Upper Morrowan) of Donets Basin. Starting from this horizon and extending into the Permian, *Lophophyllidium* and *Stereostylus*-type corals are quite common in Eurasia. They are also one of the most important components of the coral fauna in America during the same period.

Agarikophyllum was reported from beds of Westphalian D–Lower Stephanian age in the Donets Basin (Fomitshev 1953*a*). It has the same type of pseudocolumella as has commonly been reported from the Upper Pennsylvanian of the U.S.A. (Jeffords 1947) and is also observed in the Glass Mountains Permian collection.

Species assigned to the genera *Sinophyllum*, *Malonophyllum*, and *Khmerophyllum* have been reported only from the Permian. *Sinophyllum* is reported mostly from Far East Asia (e.g. Grabau 1928; Huang 1932; Fontaine 1961; Pyzhjanov 1966), *Malonophyllum* from the Permian of North America exclusively (Okulitch and Albritton 1937; Moore and Jeffords 1941), and *Khmerophyllum* from Cambodia (Fontaine 1961).

This review suggests that: (*a*) There is no interruption in the stratigraphic distribution of *Lophophyllidium*-type corals, except in the Lower and Middle Namurian, but this time period is one of the poorest known periods of tetracoral history. (*b*) The oldest known species (except *L. micula* Vojnovsky-Krieger, 1934 and *L. minimum*

Stuckenberg, 1904) have compound pseudocolumellae, which seems rather surprising. Ontogenetic studies suggest that the most primitive forms should have simple pseudocolumellae. (*c*) More complicated types of pseudocolumellae are known in the Upper Carboniferous and Permian species. No succession of development of a particular type of pseudocolumella can be traced. It is also impossible to point out which type is more advanced. The same specimen can possess several types of pseudocolumellae or different types of pseudocolumellae can appear in the same species. There is no reason to consider the structure of the pseudocolumella as a generic character.

Genus TIMORPHYLLUM Gerth, 1921

Type species. T. wanneri Gerth, 1921.

Synonyms. See Schouppé and Stacul 1955, p. 151 (*non Timorphyllum* Gerth, 1921; Moore and Jeffords 1941).
?*Timorphyllum* Gerth of Soshkina, 1941.
non Timorphyllum Gerth of Fomitshev, 1953*a*.

Diagnosis. Solitary corals with simple or compound, variable pseudocolumella and without dissepimentarium; minor septa mostly in the form of septal grooves; cardinal septum extremely short in the early neanic stage; fine structure trabecular; in longitudinal section trabeculae arranged fan-like, perpendicular to semicircular growth lines.

Remarks. The genus was discussed by Schouppé and Stacul (1955) in great detail. Regarding the micro-structure and fine-structure, the American species *T. simulans* Moore and Jeffords, 1941 (Pl. 63, fig. 3), synonymized by Schouppé (1957) with *T. wanneri ajermatiensis*, has well-developed minor septa, thus negating Moore and Jeffords's (1941) statement that they are absent. It was impossible to prepare a good longitudinal section through the septum, because the material is sparse (two specimens only), poorly preserved, and mostly silicified. However, the arrangement of the growth lines in the septa in a broken specimen is similar to *Lophophyllidium*, to which this species is now assigned.

In Soshkina, Dobroljubova, and Porfiriev 1941, Soshkina described two species from the Lower Permian of the western slope of the Urals and called them *Timorphyllum*. According to her, the Ural specimens do not have minor septa. The real generic position of these species (represented each by one specimen only) cannot be decided without careful restudy.

Timorphyllum maichense Fomitshev, 1953 from the *Doliolina* Beds of Far East Asia has all *Lophophyllidium*-type structures. However, the microstructure has not been investigated.

Schouppé and Stacul (1955) emphasized the absence of minor septa in *Timorphyllum*, supposing this character to be the main difference between *Lophophyllidium* and *Timorphyllum*. From study of many topotypes of the genus *Timorphyllum*, I concluded that most are actually monoseptal (Pl. 61, fig. 5; Pl. 62, fig. 13*e*; Pl. 63, fig. 2*a*, *b*). However, one specimen (Pl. 61, fig. 4*a*, *b*) has the surface of the external wall well preserved. On this surface there are twice as many septal grooves as there are major septa. Thus, *Timorphyllum* possesses incipient minor septa, but only as septal grooves, which are very easily destroyed during fossilization or weathering.

The ontogeny of the genus *Timorphyllum* has never been fully described. Two specimens in the Smithsonian Institution collections in which young parts are preserved are figured (Pl. 62, fig. 13*a–e*). The arrangement of septa is more or less similar to that described in *Lophophyllidium*, but the unusual shortening of the cardinal septum is noteworthy. It is so short in the youngest stage investigated (14 septa at 4·2 mm diameter) that its primary connection with the counter septum is doubtful. The true phylogenetic position of *Timorphyllum* cannot be determined without complete investigation of its ontogeny. At present one can only say that none of the *Lophophyllidium*-like species investigated has such a shortened cardinal septum in such a young ontogenetic stage. On the contrary, this septum is mostly connected with the counter during the entire neanic stage in *Lophophyllidium*.

Schouppé and Stacul (1955, text-fig. 21) show clearly the arrangement of septal growth lines in *Timorphyllum*. This arrangement may be slightly variable in the sense of more or less convexity. Some septa may be so convex that the external parts of the growth lines go down approximately 10 mm before intersecting the external wall. Schouppé and Stacul (1955) accepted Schindewolf's (1942) concept of the lamellar structure of this type of septum. The present writer cut a few topotypes more or less along the mid-lines of the septa and discovered well-developed trabeculae (Pl. 63, fig. 1) crossing few of the growth lines and arranged fan-like. The arrangement of septal growth lines and trabeculae, together with the ontogeny, are the main differences between the genera *Timorphyllum* and *Lophophyllidium*. The microstructure was also investigated in cross-section. Photography by transparent light and by scanning electron microscope gave similar results (Pl. 66, figs. 2, 3), and showed that the trabeculae are arranged almost at 90° to the mid-line of the septum, producing a structure similar to that of zigzag carinae. This structure is visible only in the middle part of the septum and is completely covered by the secondary stereoplasmatic sheets.

The information given above permits clarification of some aspects of the morphological status of the genus *Timorphyllum* and a comparison with *Lophophyllidium*. *Timorphyllum* differs from *Lophophyllidium* in its ontogeny and microstructure. Individual variability in *Timorphyllum* appears to be very great. The pseudocolumella and the axial structure are especially variable. Some topotypes have both a solitary pseudocolumella and *Verbeekiella*-like axial structure in different parts of their growth. Moreover, the change from one structure to another is not related to change in growth stage. It seems necessary to check this character as well as the relationship between *Verbeekiella* and *Wannerophyllum*, which differ only by the presence or absence of minor septa. The example of *Timorphyllum* shows that this character is very easy to miss.

CONCLUSIONS

1. The genus *Lophophyllidium* seems to be one of the most variable and widely stratigraphically and geographically distributed tetracoral genera.

2. The ontogeny of *Lophophyllidium*, with zaphrentoid arrangement of septa, elongated counter septum (and, during most of ontogeny, also the cardinal), can be compared with and related to corals of the *Fasciculophyllum omaliusi* group. The lack of a '*Calophyllum*' stage in ontogeny seems to be one of the most important differences between this genus and *Soshkineophyllum*.

3. The structure of the pseudocolumella, used hitherto as a generic character, is variable even in the same specimen. The genus is not well known in the Lower and Middle Carboniferous, and the absence of corals with *Stereostylus*-type pseudocolumella at that time does not mean that it appears only in the Upper Carboniferous. Even so, other modifications of the pseudocolumella occur at that time and transitional stages can be found.

4. The fine- and microstructure of *Lophophyllidium* and *Timorphyllum* is trabecular. The arrangement of trabeculae and the type of growth of the septa are different and should be used as generic distinctions.

5. The genus *Timorphyllum* is very similar to *Lophophyllidium* when only the macrostructure is considered. The microstructure and ontogeny indicate that they are not synonyms but homeomorphs.

6. *Timorphyllum*, in contrast to *Lophophyllidium*, seems to be endemic and characteristic only of Timor Island and Western Australia.

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JERZY FEDOROWSKI

Palaeozoological Institute
of the Polish Academy of Sciences
Poznan Branch
Poznan, ul. Mielzynskiego 27/29

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